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Benthic scavenger community composition and carrion removal in Arctic and Subarctic fjords

K. Dunlop^{1,8} · P. E. Renaud^{1,2} · J. Berge^{2,3,4} · D. O. B. Jones⁵ · R. P. Harbour⁶ · A. H. S. Tandberg⁷ · A. K. Sweetman⁶

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Abstract

In high latitude coastal regions, benthic scavenger communities are largely composed of invertebrates that play a key role in the cycling of organic matter. Factors including temperature and depth can structure Arctic and Subarctic fjord benthic communities, but the response of scavenging communities to these factors is poorly known. To address this, we compared scavenging fauna in eight fjords with different physical characteristics in Svalbard and northern Norway using time-lapse imagery of scavengers consuming Atlantic herring (*Clupea harengus*) bait. Fjords influenced by relatively warm Atlantic waters, both in Norway and Svalbard, had high scavenger richness. However, Svalbard fjords with negative bottom temperatures had the lowest species richness and were dominated by lysianassoid amphipods and ophiuroids. In these cold Svalbard fjords, the mean carrion removal rates were almost 20 times higher than mean values noted elsewhere, except in the warm Norwegian fjord Kaldfjorden. Amphipods and ophiuroids quickly reduced the bait to bones (207.6–304.7 g removed per hour (g h^{-1}); mean $290.6 \pm 7.3 \text{ g h}^{-1}$, $n=4$) in cold Svalbard fjords. In the warmer Svalbard fjords, carrion removal rates were low (0–51.5 g h^{-1} ; mean $14.6 \pm 9.0 \text{ g h}^{-1}$, $n=5$). Carrion removal rates in Kaldfjorden were higher than other Atlantic Water influenced fjords (132.1 and 372.5 g h^{-1} , $n=2$) owing to the scavenging activity of Atlantic cod (*Gadus morhua*). The results demonstrate potential ecosystem responses to warming in Arctic and Subarctic fjords, particularly effects related to range expansion of boreal species.

Keywords Arctic fjords · Benthic scavengers · Climate change · Atlantic cod

Introduction

Scavengers feed on carrion and thus play a major role in nutrient cycling and maintaining ecosystem function in marine habitats (Britton and Morton 1994; King et al. 2007).

In coastal northern high latitude waters, studies have been conducted on the community composition (Legeżyńska et al. 2000; Legeżyńska 2001; Nygård et al. 2012), population dynamics (Nygård et al. 2009, 2010) and feeding ecology (Legeżyńska 2001, 2008; Nygård et al. 2012) of shallow water scavenging amphipods. However, similar knowledge on the complete scavenger guild present in deep Arctic and Subarctic coastal waters remains limited compared to

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✉ K. Dunlop
katherine.mary.dunlop@hi.no

¹ Akvaplan-niva, 9296 Fram Centre, Tromsø, Norway

² University Centre in Svalbard, Longyearbyen, Norway

³ Department of Arctic and Marine Biology, University of Tromsø, Tromsø, Norway

⁴ Centre for Autonomous Marine Operations and Systems, Department of Biology, NTNU, Trondheim, Norway

⁵ National Oceanography Centre, University of Southampton Waterfront Campus, Southampton, UK

⁶ Marine Benthic Ecology, Biogeochemistry and In Situ Technology Research Group, The Lyell Centre for Earth and Marine Science and Technology, Heriot-Watt University, Edinburgh EH14 4AP, UK

⁷ Department of Natural History, University Museum of Bergen, University of Bergen, P.O. Box 7800, 5020 Bergen, Norway

⁸ Present Address: Institute of Marine Research, 9007 Tromsø, Norway

other marine ecosystems (i.e. the deep Pacific and Atlantic Oceans or temperate coastal regions). Studies performed in littoral and sub-littoral Svalbard waters, suggest that lysianassoid amphipods are the dominant scavenging group in some fjords (i.e. Rijpfjorden, Hornsund, Adventfjorden and Kongsfjorden) and are readily attracted to bait (Legeżyńska et al. 2000, 2001; Nygård et al. 2009, 2012). Scavenging amphipods are highly mobile and can rapidly locate carrion using highly developed chemoreceptors (Sainte-Marie 1992). A study examining the diets of lysianassoids attracted to baited traps in Kongsfjorden has demonstrated that shallow water amphipods of this superfamily rely less upon scavenging in comparison to deep-water lysianassoid amphipods (Legeżyńska et al. 2000). Arctic scavenging communities from abyssal depths (1500–5000 m) in the Fram Strait were also dominated by scavenging amphipods, in particular, the superfamilies Lysianassoidea and Stegocephaloidea (Klages et al. 2001; Premke et al. 2003, 2006). Lysianassoid amphipods of the genera *Anonyx*, *Orchomenella* and *Tmetonyx* have been caught in baited traps in Malangenfjorden in northern Norway (Christiansen and Diel-Christiansen 1993). In the deep southern Norwegian fjord Sognefjorden, scavenging amphipods attended and fed upon mackerel (*Scomber scombrus*) carcasses alongside Atlantic hagfish (*Myxine glutinosa*), pandalid shrimps and squat lobsters (*Munida tenuimana*) (Sweetman et al. 2014).

Svalbard fjords are influenced by water masses flowing northward from the Norwegian Sea (e.g. Kongsfjorden and Raudfjorden on western Svalbard), southward from the Arctic Ocean (Rijpfjorden in northern Svalbard) and from glacial meltwater (Billefjorden) (Rudels et al. 2000; Cottier et al. 2005). Water flowing northward from the Atlantic Ocean also influences fjords in northern Norway. The origin of the water masses entering the fjord has a substantial influence on the abiotic conditions of the fjords (i.e. temperature, ice coverage and salinity), which structures benthic fjord communities that inhabit these areas (Meyer et al. 2015; Molis et al. 2019). Community structure of both infauna and epifauna has been studied in Arctic fjords and has been linked to the physical characteristics of the habitat (reviewed by Molis et al. 2019). Infaunal community structure varies with the predominant water mass (Włodarska-Kowalczyk et al. 1998) among fjords/regions, but within a fjord, gradients in community structure are often driven by differences in sedimentation (from glaciers and rivers) and food supply (pigment and organic carbon content) along the fjord axes (Włodarska-Kowalczyk et al. 2005, 2012; Renaud et al. 2007). The impacts of glacial disturbance are known to decline towards the fjord mouth and to coincide with an increase in the biomass and species richness of fjord benthic macro- and megafauna (Włodarska-Kowalczyk and Pearson 2004; Włodarska-Kowalczyk et al. 2005; Jones et al. 2007; Kędra et al. 2010). Bottom water oxygen content and

organic enrichment are also known to be important factors in structuring soft-bottom benthic communities in deep-basin Subarctic fjords (Tysfjorden, Norway) (Molina et al. 2019). The community composition of the epifaunal megabenthos in two Svalbard fjords (Raudfjorden and Rijpfjorden) appears to be strongly driven by bottom water temperature and depth (Meyer et al. 2015). A broader analysis of Arctic epifaunal communities suggests that structure is also influenced by different factors on different spatial scales, from broad spatial (depth, latitude) parameters on the largest scale to habitat (water mass, substrate) and food supply characteristics on a smaller scale (Roy et al. 2014). The composition of shallow water amphipod communities and their scavenging activities in the coastal Arctic have been related to depth, hydrological conditions, sedimentation regime, bottom type, season, the presence of sea-ice and food accessibility (Legeżyńska 2001; Nygård et al. 2012).

In addition to environmental factors, the presence (or absence) of competitors and predators can also affect the distribution of benthic scavenger communities. New potential competitors and predators are expanding their distribution range into the rapidly warming Arctic sea (Renaud et al. 2015) and impacts on benthic communities have begun to be documented (Beuchel et al. 2006; Kortsch et al. 2012). The distribution of Atlantic cod (*Gadus morhua*) is dependent on water temperature (Sunby and Nakken 2008), and recent rapid climatic warming in the Arctic has also led to an expansion of Atlantic cod (and other demersal fish species) on the western coast of Svalbard since 2006 (Olsen et al. 2009; Renaud et al. 2012; Berge et al. 2015). Increased abundance and distribution of Atlantic cod may be responsible for the displacement and local extinction of native Arctic benthic and benthopelagic fish species (Fossheim et al. 2015) and to exert a major effect on both benthic and pelagic biological interactions (Renaud et al. 2012).

Scavenger communities play an integral role in the removal and recycling of carrion in many marine environments, but knowledge is limited on the full composition of marine scavenger communities in coastal Arctic regions and the abiotic factors shaping these communities. In addition, since rapidly warming Arctic temperatures can impact scavenger biodiversity and their ecosystem function, it is important to understand the connections between fjord temperature and scavenging fauna. The objectives of this study were, therefore, to investigate scavenger community composition and the role of scavengers in carrion removal in Arctic fjords and the effects of fjord abiotic factors. A baited, free-fall lander with an underwater camera system was used to study scavenger communities in fjords that experience different hydrological and environmental conditions. In the light of previous results that showed that epifaunal communities in Svalbard fjords were affected by fjord temperature (Meyer et al. 2015), it was hypothesized that scavenging

community composition and their role in carrion removal will be determined by temperature. It was also hypothesized that the composition of scavenger communities observed in the fjords will be impacted by the presence of boreal Atlantic cod.

Materials and methods

Site description

The scavenging fauna and rate of carrion removal was studied using an autonomous baited camera lander in two fjords on the northern Norwegian mainland, and six Svalbard fjords; Isfjorden, Billefjorden, Kongsfjorden, Raudfjorden, Smeerenburgfjorden and Rijpfjorden. Fjords on the mainland (Kaldfjorden and Vengsøyfjorden) and the western coast of Svalbard (Kongsfjorden, Raudfjorden, Smeerenburgfjorden and Isfjorden) are influenced by relatively warm Atlantic Water from the West Spitsbergen Current (WSC) (Svensen et al. 2002; Cottier et al. 2005; Jones et al. 2020) and are herein referred to as “warm Norwegian fjords” and “warm Svalbard fjords”. Bottom water temperatures were recorded at each site from a single SeaBird SBE 911plus CTD deployment (except in Vengsøyfjorden where triplicate ctd measurements were available) (Kaldfjorden = 6.8 °C, Vengsøyfjorden = 7.1 °C \pm 0.1 (mean \pm SE, n = 3), Kongsfjorden = 2.5 °C, Raudfjorden = − 0.5 °C, Smeerenburgfjorden = 3.5 °C and Isfjorden = 0.5 °C). Billefjorden, a fjord located in the innermost part of Isfjorden, is influenced by an influx of winter-formed cold and dense glacial meltwater that is retained by the fjord sill. This causes the bottom water temperatures to drop to as low as − 2 °C (Walkusz et al. 2003). Rijpfjorden in northeast Svalbard is influenced by cold water from the Arctic Ocean for most of the year and covered by fast ice in the winter (Walkusz et al. 2009; Hop et al. 2019). A mean bottom water temperature of − 1.9 °C \pm 0.1 (mean \pm SE, n = 3) was recorded at Rijpfjorden. Billefjorden and Rijpfjorden are herein referred to as “cold Svalbard fjords”. Site locations, depth, temperature and salinity are detailed in Fig. 1 and Online Resource 1.

Scavenger lander deployments

Time-lapse images of scavenging fauna feeding on Atlantic herring (*Clupea harengus*) carcasses at the seafloor were captured using an autonomous lander platform (KC Denmark), mounted with an Ocean Imaging Systems DSC24000 deep-sea camera. The camera used was a Nikon 7100 digital single lens reflex camera set to ISO 200, 1/25 s exposure and f-stop 8, accompanied by two strobe lights. The camera system was set to take an image every 2 min during each deployment. Before each deployment the lander

was baited with 10 freshly thawed Atlantic herring weighing 314 g (\pm 19 g), n = 10. Atlantic herring was used for its strong and oily scent, which is known to effectively attract scavengers (Schmid et al. 2017). Herring carcasses were placed inside a mesh bait bag (mesh size 1.5 cm) that was secured on to a 0.25 m² rectangular bait plate placed 150 cm directly below the camera lens (Fig. 2). The use of the mesh bag prevented scavengers from removing the bait from the camera field of view and allowed scavengers to be observed feeding on the bait throughout the deployment. Svalbard lander deployments were conducted during the day and night between the 8th and 18th of August 2017 from the RV *Helmer Hanssen* (UiT, The Arctic University of Norway). Lander deployments were conducted across a range of depths from 145 m in Smeerenburgfjorden to 360 m water depth in Kongsfjorden. A single camera lander deployment was made in each fjord except Rijpfjorden (3 replicates) (Online Resource 1). Lander deployments were also made in the warm Norwegian fjords from the RV *Johan Hjort* (Institute of Marine Research, Norway) between the 30th of November and the 2nd of December 2017. Camera lander deployments in Vengsøyfjorden were made at a water depth of 275 m (\pm 2 m, n = 3), and in Kaldfjorden at a depth of 171.5 m (\pm 5 m, n = 2) (Online Resource 1). The lander was deployed onto relatively flat seabed in each fjord basin. However, as the geomorphology of each study fjord varied it was only possible to standardize depth as much as possible. The duration of deployments varied from 26 h 11 min (Kongsfjorden) to 7 h and 7 min (Smeerenburgfjorden). Prior to each lander deployment, sensor-based water conductivity, temperature (°C) and depth (m) data were collected. Immediately following each lander recovery, scavenging lysianassoid amphipods that remained on the lander bait plate were removed and preserved in 4% buffered formaldehyde seawater. Remaining herring carcass fragments were removed, dissected to collect scavengers buried in the flesh, blotted dry and weighed to determine the weight of the herring mass removed by the scavengers.

Demersal fish trawls

Demersal trawls were made in all Svalbard fjords, except Billefjorden, from the RV *Helmer Hanssen*. Trawling was at a speed of 3 knots with a Campelen trawl (opening of 1.7 m) and was conducted on the same date as the lander deployments in the Svalbard fjords (trawl details are reported in full in Online Resource 2). Trawl distances ranged between 0.9 and 2.2 km and in all cases were less than 5 km from the lander positions. Demersal trawls in Vengsøyfjorden (n = 2) and in Kaldfjorden (n = 1) were made on the 2nd and 3rd of April 2019 from the RV *Helmer Hanssen* and each trawl was

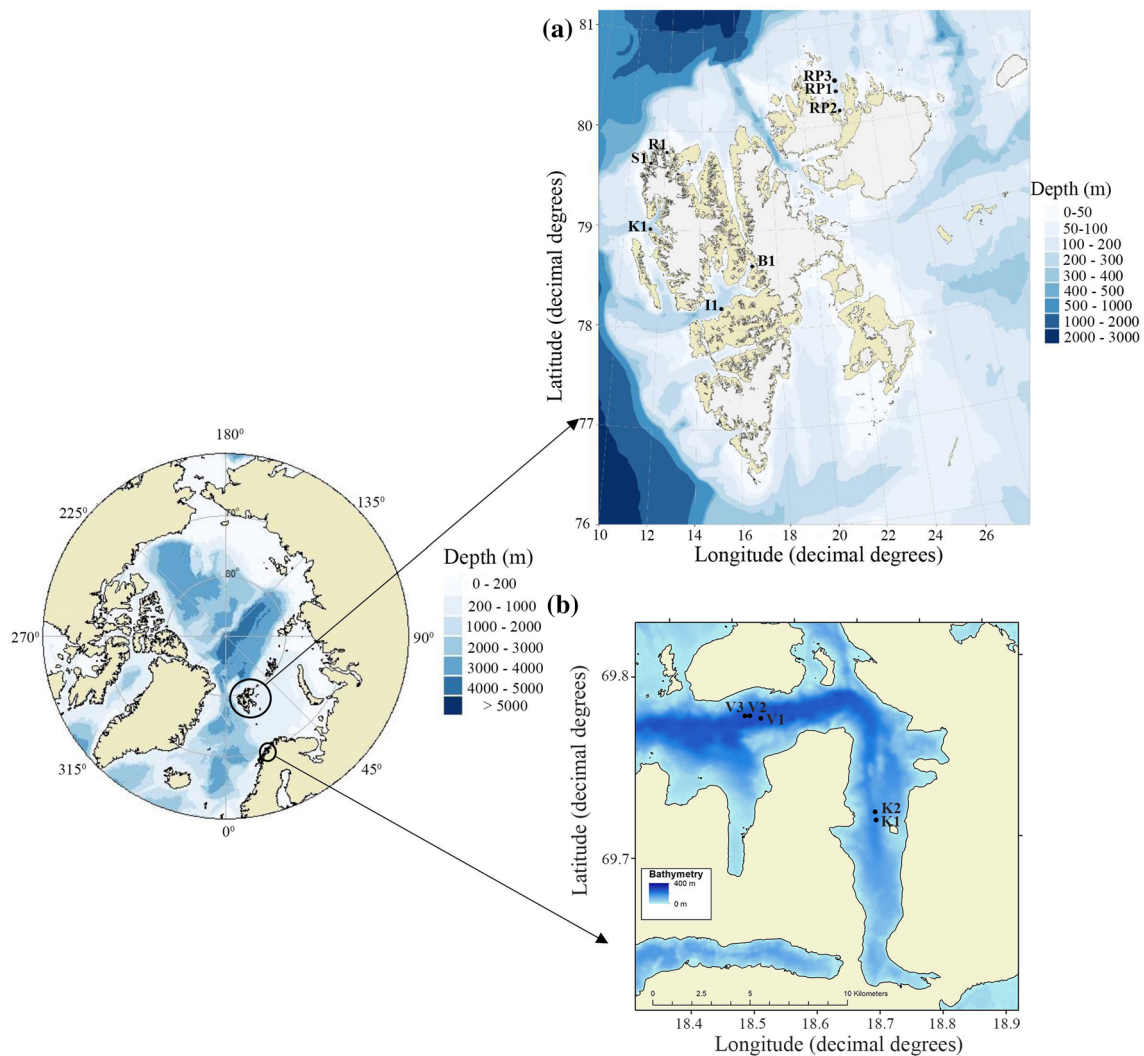


Fig. 1 Camera lander deployment sites in **a** Kongsfjorden (K1), Raudfjorden (R1), Rijpfjorden (Rp1, Rp2, Rp3), Smeerenburgfjorden (S1), Isfjorden (I1), Billefjorden (B1) and **b** Vengsøyfjorden (V1, V2, V3) and Kaldfjorden (K1, K2)

over a distance of 1 km, at a speed of 3 knots and in close proximity (> 1 km) to the lander positions.

Image and data analysis

Images from all 13 lander deployments were viewed in Adobe Photoshop CC 2018. Individuals on the bait plate were considered as scavengers and were identified to the lowest taxonomic level. The number of individuals from each species or taxon were counted for the first 7 h of each lander deployment. This duration corresponded to the shortest lander deployment (in Smeerenburgfjorden). A semi-automated counting tool, as described in Beuchel et al. (2010), was used to quantify individual amphipods. The technique worked for images where individual amphipods were well separated (i.e. in images recorded in Kongsfjorden and early in the lander deployments in Rijpfjorden

and Billefjorden) where the algorithm could distinguish among individual animals. However, in images with dense aggregations of amphipods, the manual Count Tool (Adobe Photoshop CC 2018) was used to annotate images. The hering flesh was consumed as the deployment advanced and showed that some amphipods had been inside and under the flesh and masked during counting. Therefore, amphipod counts represent a minimum abundance. All amphipods in the images were considered as *Lysianassoidea* based on specimen identification.

The maximum number of scavengers observed at the bait (Max_N), the time between the arrival of the lander on the seafloor and the arrival of the first scavenger (t_{arrival}) are recognized proxies of scavenger abundance (Willis and Babcock 2000; Yeh and Drazen 2009; Langlois et al. 2018). Mean Max_N and t_{arrival} values are written \pm standard error in the results, unless otherwise stated. These parameters were

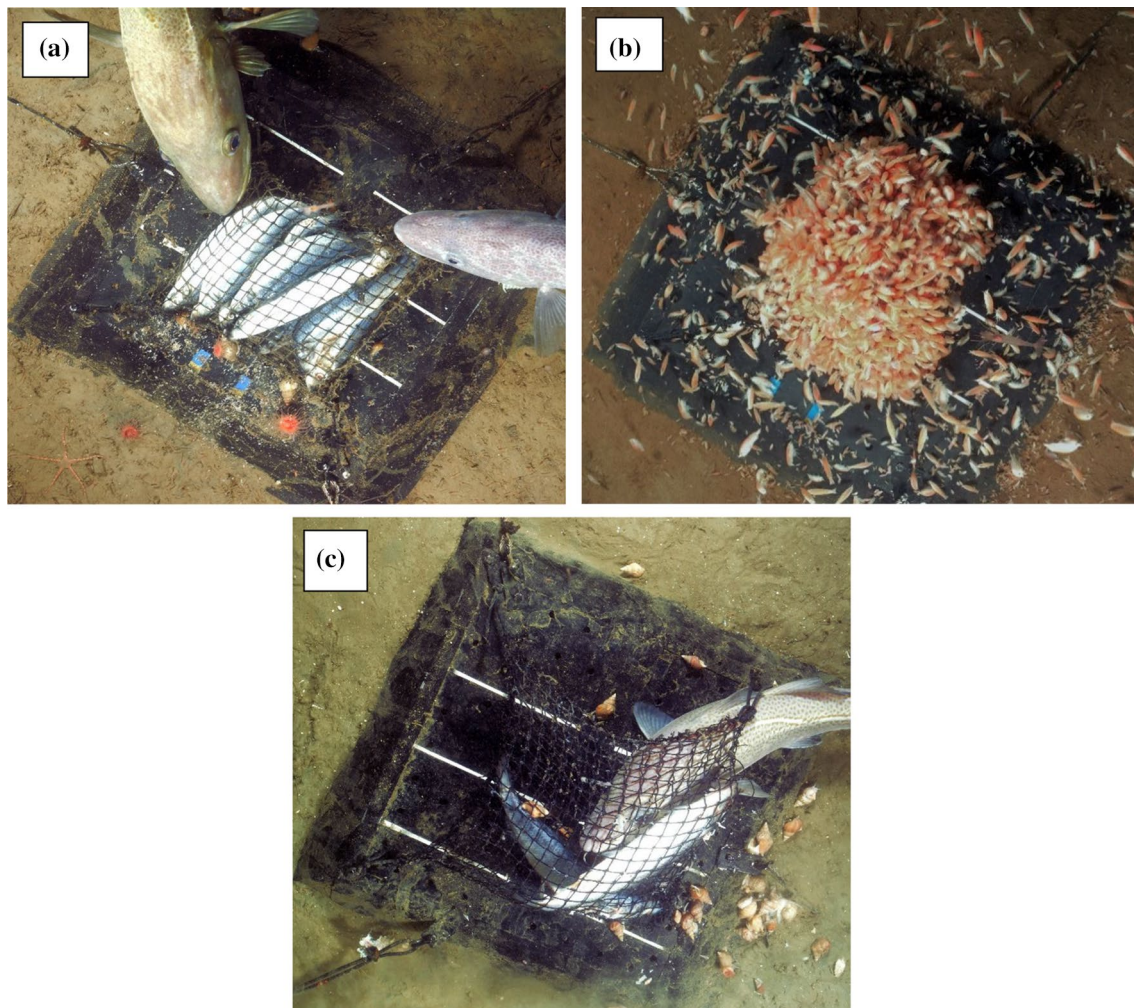


Fig. 2 Lander images of **a** Atlantic cod (*Gadus morhua*) investigating the Atlantic herring bait (*Clupea harengus*) in Kongsfjorden, Svalbard, **b** A lysianassoid amphipod swarm feeding on herring bait

in Rijpfjorden, Svalbard and **c** Atlantic cod removing herring bait in Kaldfjorden, Troms, Norway

calculated for each deployment. Scavenging rates were calculated by dividing the change in the weight of the herring bait (if any bait remained on the bait plate upon retrieval) by the deployment duration. However, if all the bait flesh was consumed before the end of the deployment, the scavenging rate was calculated by dividing the bait weight at the beginning of the deployment (minus the skeleton weight at the end) by the time it took for the bait to be completely removed (as observed in the sequence of images).

Statistical analysis

Scavenger assemblage data between fjords were analysed using the statistical package PRIMER-E v7 (Clarke and Gorley 2015) using Max_N as a proxy for abundance. For each fjord, the total number of fauna, species richness, Shannon diversity (log base e) and the Pielou evenness index were

calculated for scavenger communities. Multivariate analysis was performed using Bray–Curtis dissimilarity coefficients on fourth-root transformed data (transformed to reduce the right skew of the data). A principal coordinates analysis (PCoA) was used to visually examine how fjord depth, temperature, salinity and Atlantic cod abundance (from demersal trawls) structured scavenger assemblage composition in the different fjords. Distance-based linear modelling (DISTLM) analysis was used to examine the relationship between scavenger communities and environmental predictors. Further multivariate analysis was performed in PRIMER-E to examine whether there were differences in scavenger community composition between fjords that were seen to be separated in the PCoA analysis. A univariate statistical analysis was performed on bait consumption rates using the software package R (version 3.3.2; R Core Team 2016). Data on the bait consumption rate did not meet the statistical parametric

assumptions and thus a non-parametric Kruskal–Wallis test was used to analyse the effect of the fjord temperature on scavenging rates.

Results

Atlantic cod abundances

Atlantic cod was a prominent species in the trawl catches in all fjords influenced by Atlantic Water (warm Norwegian and Svalbard fjords). The highest cod abundances were recorded in Raudfjorden and Kongsfjorden (mean 15,000 and 6000 individuals km², respectively). Cod were also present in other fjords, but in lower numbers (between 1188 and 4250 individuals km²). In Rijpfjorden, which is dominated by cold water masses, Atlantic cod were not caught (Online Resource 2).

Scavenger community composition

Thirty-two scavenger taxa were identified from 13 baited lander deployments in the 8 study fjords (Table 1). At least 16 of these taxa were attracted to the bait in the warm Svalbard fjords including several fish (*G. morhua*; *Hippoglossoides platessoides* and *Raja radiata*) and crustaceans taxa (*Hyas araneus*, *Pandalus* sp. and *Pagurus pubescens*) (Fig. 2a, Table 1). Three taxa were attracted to the bait in Raudfjorden, which was lower compared to the 6 to 11 taxa observed in the other warm Svalbard and warm Norwegian fjord deployments (Table 1). The abundance of scavengers was highest in Kongsfjorden, compared to the other warm Svalbard fjords, and reached a Max_N of 242 near the end of the lander deployment (Fig. 3a). Shrimp of the genus *Pandalus* were the first scavengers to arrive in deployments in the warm Svalbard fjords, arriving after 2 to 8 min in Kongsfjorden, Smeerenburgfjorden and Isfjorden and

Table 1 Scavenger species observed at the lander bait in each deployment site and corresponding maximum abundance (Max_N)

Scavenger Species	Kongsfjorden	Raudfjorden	Smeerenburgfjorden	Isfjorden	Vengsøyfjorden	Kaldfjorden	Billefjorden	Rijpfjorden
<i>Ophiura albida</i>	0	0	0	0	1	1	0	0
<i>Ophiopleura borealis</i>	0	0	0	0	0	0	0	73
<i>Ophiura sarsii</i>	2	0	6	0	0	0	0	0
<i>Ophiocten sericeum</i>	0	0	0	0	0	0	52	0
Amphipods (<i>Anonyx nugax</i> , <i>Anonyx makarovi</i> , <i>Socarnes bidenticulatus</i> , <i>Tmetonyx</i> sp., <i>Centromedon productus</i> , <i>Onisimus affinis</i>)	0	0	0	0	0	0	164	1160
Amphipods (<i>Anonyx lilljeborgi</i> , <i>Scope-locheirus crenatus</i> , <i>Tryphosidae</i> ind sp. A, <i>Tryphosidae</i> ind sp. B)	0	0	0	0	0	65	0	0
Amphipods (unidentified)	242	0	0	0	0	0	0	0
<i>Gadus morhua</i>	2	0	0	1	2	4	0	0
<i>Hippoglossoides platessoides</i>	1	0	0	1	0	0	0	0
<i>Raja radiata</i>	1	0	0	0	0	0	0	0
<i>Brosme brosme</i>	0	0	0	0	1	0	0	0
<i>Liparis</i> sp.	0	0	0	1	0	0	0	0
<i>Boreogadus saida</i>	0	0	0	0	0	0	2	1
<i>Pandalus</i> sp.	9	25	30	6	1	1	0	2
<i>Hyas araneus</i>	0	2	2	0	0	0	0	0
<i>Pagurus pubescens</i>	0	0	2	0	0	0	0	0
<i>Mysida</i> sp.	8	0	2	4	0	0	0	0
<i>Buccinum undatum</i>	1	0	5	0	0	38	0	0
Prosobranch	13	0	0	0	0	0	0	0
Nemertean	5	1	0	2	1	8	0	0
<i>Urasterias lincki</i>	0	0	0	0	0	0	0	1
<i>Chaetognatha</i> sp.	1	0	0	0	0	0	0	0
<i>Polychaeta errantia</i>	0	0	0	4	0	0	0	0
<i>Polycirrus arcticus</i>	0	0	0	1	0	0	3	0

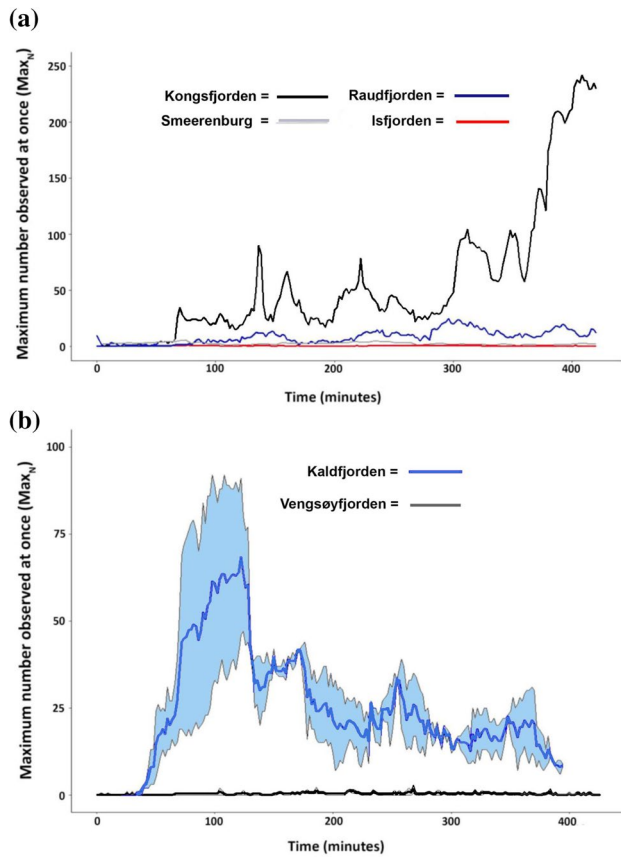


Fig. 3 Mean maximum number (\pm SE) of the total scavengers observed in **a** Kongsfjorden (black line), Raudfjorden (blue line), Smeerenburgfjorden (grey line) and Isfjorden (red line), and **b** Kaldfjorden (blue line (mean \pm S.E.)) and Vengsøyfjorden (black line (mean \pm S.E.))

after 64 min in Raudfjorden and reached a mean Max_N of 17.5 ± 5.9 individuals ($n=4$) (Table 1). Aggregations of lysianassoid amphipods arrived at the bait in Kongsfjorden but appeared to have a limited role in carrion consumption based on the low amount of herring consumed. At least 7 scavenger taxa were attracted to the bait in both the warm Norwegian fjords (Table 1). *Buccinum undatum* and lysianassoid amphipods dominated in Kaldfjorden, and both taxa arrived after approximately 40 min. *B. undatum* reached a mean peak of 36.5 ± 1.5 individuals at 193 ± 27 min ($n=2$) and lysianassoid amphipods peaked at a Max_N of 40.5 ± 24.5 individuals at 94.5 ± 27.5 min ($n=2$) (Fig. 3b). Lysianassoid amphipod aggregations arrived at the bait after 26 and 30 min and included the species; *Scopelocheirus crenatus*, *Anonyx lilljeborgi* and 2 species from the genus *Tryphosidae* (identified from the amphipod samples). The Max_N of Atlantic cod was highest in Kaldfjorden and reached a mean of 3.5 ± 0.5 individuals ($n=2$) (Fig. 2c). Scavenger abundances in Vengsøyfjorden were the lowest of all fjords with a mean total Max_N of 3.3 ± 0.3 individuals ($n=3$) and a mean t_{arrival}

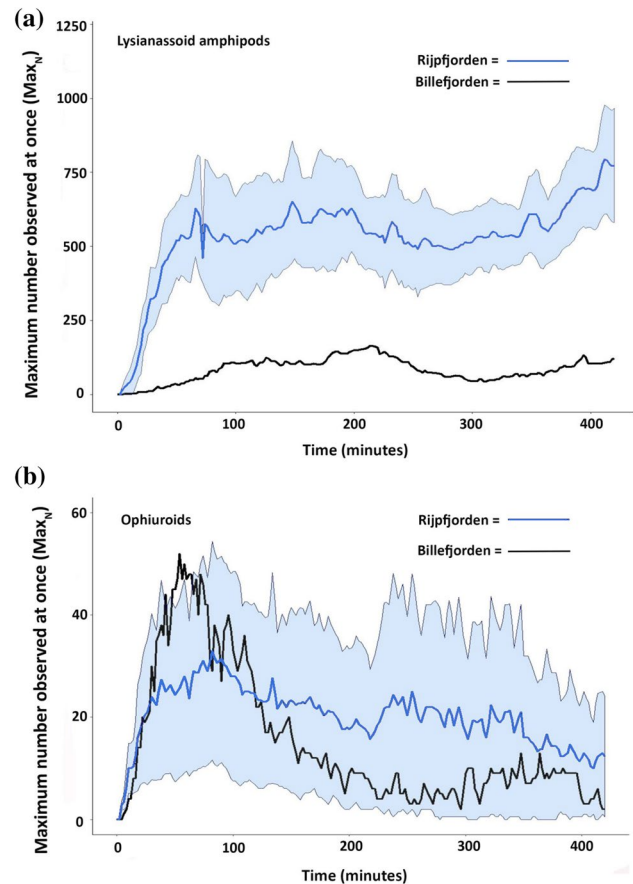


Fig. 4 Mean maximum number (\pm SE) of **a** lysianassoid amphipod and **b** ophiuroids observed at any one time during lander deployments (Max_N) in Rippfjorden (blue line (mean \pm S.E.)) and Billefjorden (black line)

of $113 (\pm 53.8)$ minutes (Fig. 3b). Scavenger communities in Vengsøyfjorden were comprised of *G. morhua*, *Brosme brosme*, *Pandalus* sp., *Ophiura albida* and a Nemertean worm (Table 1).

In the cold Svalbard fjords lysianassoid amphipods and ophiuroids (*Ophiocten sericeum* and *Ophiopleura borealis*) dominated the scavenging taxa in all deployments (Fig. 2b). In all three Rippfjorden deployments, *O. borealis* and lysianassoid amphipods arrived within minutes of the lander reaching the sea floor (t_{arrival} , 7.3 ± 3.3 min and 13.3 ± 5.9 min, $n=3$) (Fig. 4a, b). Lysianassoid amphipods identified at the bait in Rippfjorden included the taxa; *Onisimus affinis*, *Anonyx nugax*, *Anonyx makarovi*, *Socarnes bidenticulatus*, *Centromedon productus* and *Tmetonyx* sp. (identified from the amphipod samples). *O. borealis* numbers peaked earlier than the amphipods with numbers reaching a peak Max_N of 26 individuals in 60 min in deployment 1 and 73 individuals in 56 min in deployment 2. However, only a single *O. borealis* arrived (after 14 min) at the bait in the final Rippfjorden deployment. In all Rippfjorden

deployments, lysianassoid amphipod numbers continued to increase with time, peaking at a Max_N of 817.7 ± 175.0 individuals ($n=3$) after 416 ± 4 min. Lysianassoid amphipods and *O. sericeum* were the first taxa to arrive at the bait in Billefjorden (t_{arrival} : 6 and 8 min respectively) after the lander reached the seafloor. Amphipod numbers increased to a peak of Max_N of 164 individuals at 216 min and *O. sericeum* to a Max_N of 52 individuals at 72 min (Fig. 4a, b). In deployments in both cold Svalbard fjords, ophiuroids moved off the bait plate to form aggregations on the adjacent sediments as lysianassoid amphipod numbers and feeding activity increased. In addition to lysianassoid amphipods and the 2 ophiuroid species, 4 other scavenger taxa were attracted to the bait in the cold Svalbard fjords (*Boreogadus saida*, *Pandalus* sp., *Urasterias lincki* and *Polycirrus arcticus*). The number of taxa and evenness index were, in general, lower in the cold Svalbard fjords compared to the other six fjords studied (Table 2).

In Kongsfjorden and Raudfjorden herring carcasses were consumed at 32.3 g h^{-1} and 51.5 g h^{-1} but in Smeerenburgfjorden, Isfjorden and Vengsøyfjorden almost no scavenging of the herring bait occurred ($0\text{--}2 \text{ g consumed h}^{-1}$) (Fig. 5). Herring carcasses were, however, rapidly consumed by ophiuroids and lysianassoid amphipods in Rijpfjorden ($284.5 \pm 7.4 \text{ g h}^{-1}$, $n=3$) and Billefjorden (207.6 g h^{-1} , $n=1$) (Fig. 5). The mean scavenging rates in the cold Svalbard fjords were significantly higher compared to rates in the other six fjords studied ($55.1 \pm 38.8 \text{ g h}^{-1}$, $n=10$) (Kruskal–Wallis test, $H_2=8.1$, $p=0.02$). Carrion removal rates in the cold Svalbard fjords were 19.9 times higher than in Kongsfjorden, Raudfjorden, Smeerenburgfjorden, Isfjorden and Vengsøyfjorden where rates were almost zero to 51.5 g h^{-1} (mean $14.6 \pm 9.0 \text{ g h}^{-1}$). Carrion removal rates in Kaldfjorden (132.1 and 372.5 g h^{-1}) were, however, higher than in the other warm Svalbard and Norwegian fjords and more similar to the scavenging rates observed in the cold Svalbard fjords owing to the scavenging activity of Atlantic cod (Fig. 5).

Table 2 Number of species, species diversity (Shannon–Wiener Index) and evenness (Pielou Index) recorded in each fjord

Fjord	Number of taxa	Species diversity (Shannon–Wiener)	Evenness (Pielou Index)
Kongsfjorden	11	0.628	0.262
Raudfjorden	3	0.409	0.372
Smeerenburg	6	1.516	0.729
Isfjorden	8	1.834	0.882
Billefjorden	4	0.663	0.478
Rijpfjorden	5	0.187	0.213
Kaldfjorden	6	0.868	0.606
Vengsøyfjorden	5	1.629	0.987

The composition of scavenger communities showed a clear separation in the PCoA plot between the warm Svalbard and Norwegian fjords and the cold Svalbard fjords (Fig. 6). The PCoA cumulatively explained 63.8% of the variation in the scavenger communities, with temperature at the seafloor, cod abundance and salinity identified as major drivers structuring scavenger community composition. The multivariate regression analysis using DISTLM indicated that the predictor variables, fjord temperature, cod abundance and salinity, best explained the total variation of the scavenger community composition (Table 3). Fjord temperature explained the

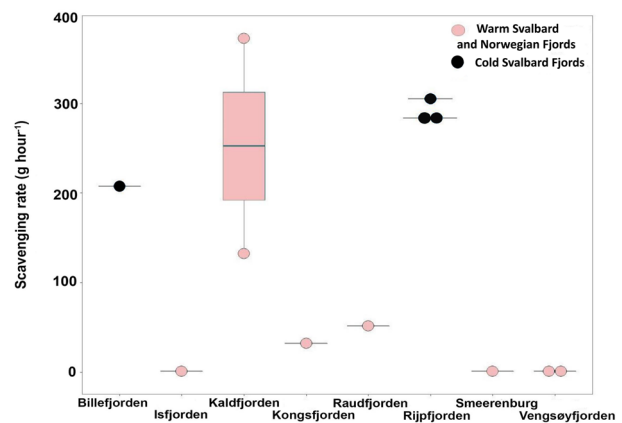


Fig. 5 Wet weight consumption rates (\pm SE) of herring carcasses in the six warm Svalbard and Norwegian fjords and two cold Svalbard fjords

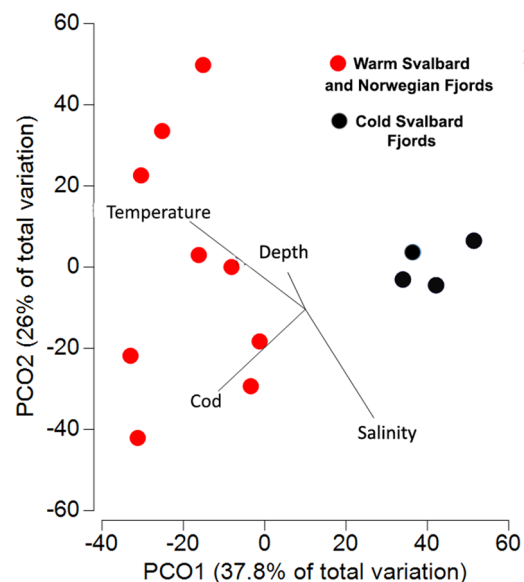


Fig. 6 A principal coordinates analysis ordination of sampled scavenger community composition in warm Svalbard and Norwegian fjords and cold Svalbard fjords

Table 3 DISTLM modelling results to determine the correlations between scavenger community composition and the environmental variables; Temperature, Cod Abundance, Salinity and Depth

Variable	R^2	SS (trace)	Pseudo- F	p	Proportion	Cumulative	Residual degrees of freedom
Temperature	0.271	7969.4	4.089	0.003	0.271	0.271	11
Cod Abundance	0.441	4989.3	3.033	0.018	0.170	0.441	10
Salinity	0.549	3196.9	2.171	0.044	0.109	0.549	9
Depth	0.622	2127.6	1.530	0.187	0.072	0.622	8

greatest amount of the variation (27.1%) (forward selection sequential tests) (pseudo- $F_{11}=4.09$, $p=0.003$), followed by cod abundance (17.0%; pseudo- $F_{10}=3.03$, $p=0.018$) and salinity (10.9%; pseudo- $F_9=2.17$, $p=0.05$). While depth explained 7.0% of the variation in the scavenger community composition it did not explain a significant proportion of the variation. The predictor variables (fjord temperature, cod abundance, salinity and depth) explained 62.2% of the total variation in scavenger community composition (Table 3). The differences in scavenger community composition between the warmer and colder fjords was further explored with a PERMANOVA analysis and found to be significant (PERMANOVA, pseudo- $F_1=2.60$, $p=0.05$). Lysianassoid amphipods had the highest average abundance in the cold Svalbard fjords and contribution (SIMPER analysis; 51.0%) to the dissimilarity between these and the other six fjords. This was followed by the ophiuroids, *O. borealis* (SIMPER analysis; 17.8% dissimilarity) and *O. sericeum* (SIMPER analysis; 6.1% dissimilarity). *Pandalus* sp., *B. undatum*, *G. morhua* and *Nemertea* sp. contributed to the highest average abundance of scavengers in the six Atlantic water influenced fjords. These taxa contributed 4.9, 3.7, 2.7 and 2.3% to the dissimilarity between these fjords and the scavenger community composition observed in the cold Svalbard fjords (Online Resource 3).

Discussion

This study represents one of the most comprehensive investigations of benthic invertebrate and demersal fish scavengers in high Arctic and Subarctic fjords to date. Results demonstrate a distinct difference in benthic scavenging assemblages between study fjords with differing hydrological and environmental conditions. In general, a greater number of taxa, from a greater range of scavenger groups (Fish, Crustaceans, Molluscs, Echinoderms, Nemertean and Polychaetes) were attracted to the bait in the fjords influenced by the relatively warm Atlantic Water, compared to fjords dominated by cold water masses. However, in these relatively warmer fjords there was a significantly lower abundance of scavengers and a lower removal rate of herring carcasses. In Rjipfjorden and Billefjorden, large abundances of specialized

scavengers, such as lysianassoid amphipods and ophiuroids, quickly aggregated and consumed the herring bait.

The results presented here suggest that fjord temperature has a significant effect on the benthic scavenger community. The impact of temperature and duration of sea-ice-cover on the structure of benthic communities has previously been documented for infauna and epifauna in Svalbard fjords (Beuchel et al. 2006; Kędra et al. 2010; Kortsch et al. 2015; Meyer et al. 2015). Water temperature and depth were found to be major drivers of epibenthic megafaunal community composition between the warmer Atlantic Water influenced fjord Raudfjorden and the Arctic Water influenced fjord Rjipfjorden (Meyer et al. 2015). The study of Meyer et al. (2015) indicated a lower diversity and abundance of benthic megafauna species in Raudfjorden compared to Rjipfjorden. Our study on the scavenging fauna in 8 fjords also found lower species richness in Raudfjorden, but the relationship between diversity and temperature was not consistent as scavenger richness in Raudfjorden was lower than the other Atlantic Water fjords. Depth differences among stations had limited influence both on scavenger community abundance and composition in this study. The stark contrasts in scavenger communities between warm and cold Svalbard fjords, however, suggest that depth is unlikely to be the dominant factor here.

In consideration of our results and those of previous studies, it is clear that warmer temperatures have enabled more boreal species to exist in Atlantic Water influenced fjords. This process has contributed to a greater number and higher diversity of demersal fish and benthic invertebrate taxa identified in Atlantic Water fjords (Fossheim et al. 2015; Renaud et al. 2015). The boreal taxa observed in this study included *G. morhua*, *H. platessoides*, *B. brosme*, *Pandalus* sp., *H. araneus*, *P. pubescens* and *B. undatum*. Many of these boreal taxa are generalist feeders and can be described as predators, as well as facultative scavengers, as is common with many species attending carrion on the seafloor (Britton and Morton 1994; Ruxton and Houston 2004). This opportunistic strategy allows these scavengers to effectively utilize a range of food sources in the fjords, including carrion. Specialized scavengers are highly adapted to detect, locate and remove carrion (Ruxton and Houston 2004) and it is logical that these generalist boreal species can be less adapted to rapidly

detect and utilize the bait. Low numbers of generalist scavenger taxa observed at the bait is likely to have led to lower scavenging rates in the warmer Atlantic Water influenced fjords. Rjipfjorden and Billefjorden are both influenced by colder winter-formed bottom water that is formed during ice formation and brine rejection and glacial meltwater in the innermost basins of the fjord, respectively. However, they supported a few highly specialized scavenger groups (lysianassoid amphipods and scavenging ophiuroids). These abundant taxa were able to rapidly detect carrion, aggregate in large numbers and remove carrion rapidly. The carrion removal rates in these cold Svalbard fjords were substantially higher than scavenging rates on mackerel in the southern Norwegian fjord Sognefjorden (57.8 g h^{-1}) (Sweetman et al. 2014). Rates are, however, comparable to the speed at which fish bait was removed by scavenging Arctic amphipods in the Fram Strait (Arctic Ocean) (Premke et al. 2003). The rapid removal of carrion in the cold Svalbard fjords by benthic invertebrates can be considered as an adaptive trait to cope with seasonal differences in food availability in these periodically ice-covered fjords.

The distribution of Atlantic cod is dependent on water temperature (Sunby and Nakken 2008), and cod are now established in the warm Svalbard and northern Norwegian fjords studied, as confirmed by the trawl data from this study. The low bottom water temperatures in the two cold Svalbard fjords likely prevent Atlantic cod from achieving high densities. Atlantic cod feed on a wide range of benthic prey, including amphipods and echinoderms (Hüssy et al. 1997; Schwalme and Chouinard 1999; Link and Garrison 2002; Dalpadado and Bogstad 2004; Dalpadado et al. 2009). The increased abundance and distribution of Atlantic cod in the Arctic, therefore, has the potential to affect Arctic scavenger populations dominated by lysianassoid amphipods and Echinoderms. The lysianassoid amphipods play a key role in polar environments by transferring the energy contained in dead organic material to higher trophic levels (Sainte-Marie 1992; Jazdzewski et al. 1995). The role of amphipods in carrion consumption will be reduced if they have been removed by cod and their numbers diminished. This can lead to an alteration in pathways of energy transfer through the fjord food web or alternatively to other genera filling the role of scavengers. This study does not present a time-series dataset on scavenger communities in the study fjords, but lysianassoids amphipods are also known to be highly abundant in the shallow waters of the warm Atlantic Water influenced Svalbard fjords; Adventfjorden (Nygård et al. 2009, 2010, 2012) Hornsund (Legeżyńska et al. 2000) and Kongsfjorden (Legeżyńska 2001). Baited traps, deployed in 2007 and 2008, also found that lysianassoid amphipods of the genus *Anonyx* dominated the scavenging fauna in Rjipfjorden (Nygård et al. 2012). Invertebrate scavengers (Crustaceans, Gastropods and Nemertean worms) were observed

alongside fish fauna in the warm Svalbard fjords; however, their numbers were low (< 50 at one time) compared to the cold Svalbard fjords. Invertebrate scavengers in warm Svalbard fjords appeared to have limited capacity to remove carrion and can also be subject to Atlantic cod predation, which provides a flow on energy from carrion to higher trophic levels.

In Kaldfjorden, Atlantic cod played a greater role in carrion removal and were responsible for high scavenging rates here, demonstrating that Atlantic cod can act as a scavenger, albeit a facultative one. In Kaldfjorden, Atlantic cod were observed to suck the bait into their mouths and to take large bites to remove the bait from the bag. Similar feeding behaviour of Atlantic cod has been observed (Jones 1978; Løkkeborg et al. 1998), and this behaviour can attract other cod (Brawn 1969). High scavenging rates from cod could also be connected to the concentrations of whelks that were attracted to and fed on the bait. In some cases, whelks appeared to have opened the herring carcasses, perhaps enhancing the odour plume and thereby attracting more Atlantic cod and other scavengers. Kaldfjorden experienced large influxes of Atlantic herring, and humpback whales (*Megaptera novaeangliae*) feeding on the herring, in the winters between 2012 and 2017 (Bakketeig et al. 2016; Zubiri 2017). Feeding by the whales caused the accumulation of many herring carcasses on the seafloor. The availability of fish carcasses on the seafloor in the winter from whale feeding and fishing discards are possible explanations for the adaptation of Atlantic cod in Kaldfjorden to scavenging.

Position within the fjord is known to affect benthic community composition through the influences of differences in sedimentation and food supply (Włodarska-Kowalczyk et al. 2005, 2012) but this was not studied here as an environmental parameter that could potentially effect scavenger community composition. In an effort to sample as many different fjords as possible, we were unable to replicate deployments along fjord gradients in fjords other than Rjipfjorden. The consistency of results here, however, suggests that the fjord basin selected (when more than one exists) may not have a strong influence on scavenger communities in many fjords. One possible exception could be the strongly glacially influenced Billefjorden, and, whereas scavenger community composition here differed from the other cold fjord (Rjipfjorden), scavenging rates were comparable despite the potentially strong influence of the glacier.

The Arctic is warming rapidly (Stocker et al. 2013; Sweetman et al. 2017) and there is a clear need to understand the implications of fjord temperature on scavenger communities and the potential impacts on their role on benthic fjord processes. Arctic and Subarctic fjords are experiencing both rapid warming and growing numbers of boreal species (such as Atlantic cod). It has been shown in this study that high Arctic and Subarctic fjords influenced by warmer Atlantic

Water contain scavenger communities that are more diverse but of lower abundance than high Arctic fjords influenced by winter-formed bottom water. These colder water fjords support highly abundant scavenger assemblages of lysianassoid amphipods and ophiuroids that rapidly processed sunken carrion. This study demonstrates the potential impacts of warming Arctic temperatures, and associated shifts in predatory fish, on Arctic and Subarctic fjord benthic scavenging fauna and their role in benthic energy and nutrient cycling. These processes may indirectly alter scavenger efficiency in some fjords and potentially lead to an alteration in pathways of energy transfer through the fjord food webs.

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Author contributions KD, AKS, DOBJ, RPH, JB and PER conducted the field work and data collection, KD analysed the images and conducted the data analysis, AHST identified the amphipod specimens. All authors were involved in writing and editing various versions of the manuscript.

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Data availability All data included in this paper is available on Mendeley Data.

Compliance with ethical standards

Conflict of interest It is confirmed that as far as the authors are aware no conflict of interest exists regarding this manuscript.

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